

## Remote, Inland Occurrence of the Oceanic *Anogramma leptophylla* (L.) Link (Pteridaceae: Taenitidoideae) in Hungary

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**ABSTRACT.**—The presence of the fern species *Anogramma leptophylla* was detected in the Zempléni Mountains (NE Hungary) in 1991. The species was known neither from the country nor from the whole Carpatho-Pannonian Region (also known as Carpathian Basin) previously. Its habitat is situated on a roadside bank, cut into an unstable rhyolite surface, above the valley of the Creek Kemence near the village of Pálháza. The fern is a cosmopolitan taxon restricted to humid environments and is considered to be an oceanic-suboceanic (Atlantic) element in Europe. The occurrence in Hungary is located more than 1000 km from the closest populations, thus, this is one of the most remote inland occurrences of this (sub)oceanic species. This striking presence of the fern may be due to the peculiar microclimatological conditions of the habitat, which are described here in order to give an exact explanation for this outstanding occurrence. The chromosomes were also counted in some individuals of the Hungarian population and were found to be  $n=26^{II}$  for each sample.

**KEY WORDS.**—leptokurtic dispersal event, pteridoflora of Europe, microclimatic characterization of habitat, chromosome count, range expansion, *Anogramma leptophylla*

In 1991, a population of a small fern species was found in Hungary for the first time by Sz. Zólyomi in the Zempléni Mountains (Hungarian spelling: Zempléni-hegység). The species was identified as *Anogramma leptophylla* (L.) Link (Pteridaceae, Taenitidoideae; Tyron *et al.*, 1990; Sánchez-Baracaldo, 2004) using the “Collectio Pteridophytorum” of the Hungarian Natural History Museum (BP) and by counting the chromosomes. The species has not been reported previously from the Carpatho-Pannonian Region (also known as

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FIG. 1. Distribution of *Anogramma leptophylla* in Europe. The newly found Hungarian population is indicated by square. Modified after Jalas and Suominen (1972).

Carpathian Basin). Thus, with its unusual short life cycle and annual sporophyte, *A. leptophylla* can be considered one of the most extraordinary members of the flora of the region.

The gene center of the genus *Anogramma* (*sensu* Tryon *et al.*, 1990) is located in Central and South America, where all *Anogramma* species except *A. ascensionis* (Hook.) Diels can be found, including cosmopolitan *A. leptophylla*. *Anogramma caespitosa* Pic.Serm. reported from Tanzania was recently reduced to synonymy under *A. leptophylla* (Nakazato and Gastony, 2003). *Anogramma leptophylla* can be found in many humid and mild regions around the world. Besides the Americas, the range of the species includes the subtropical regions and coastal regions of Africa, and the subtropical regions of Australia and Oceania. Its distribution range extends from Iran to Malaysia in Asia, and it also inhabits the southern portion of the Himalayas, the Caucasus and the Middle East. In Europe, it occurs in the Mediterranean region, along the Atlantic coast, the Mediterranean basin and in Crimea (Fig. 1; Jalas and Suominen, 1972; Komarov, 1934; Pignatti, 1982; Castroviejo *et al.*, 1986; Prelli, 1990; Stace, 1997).

The European distribution pattern of the species shows a conspicuous preference for humid regions, and it is considered to be an oceanic-suboceanic element (Meusel *et al.*, 1965; Dostál, 1984). In the western territories it grows in coastal regions and mountains under oceanic climatic influence, whereas the vast majority of the eastern (i.e., suboceanic) occurrences is restricted to the shores of the Mediterranean Sea (Dostál, 1984). Some inland occurrences have also been detected, but these are either under oceanic influence or influenced by local microclimatic conditions. This pioneer species prefers competition-free habitats, where it inhabits rock surfaces and crevices (Page, 1982; Jermy and Camus, 1991).



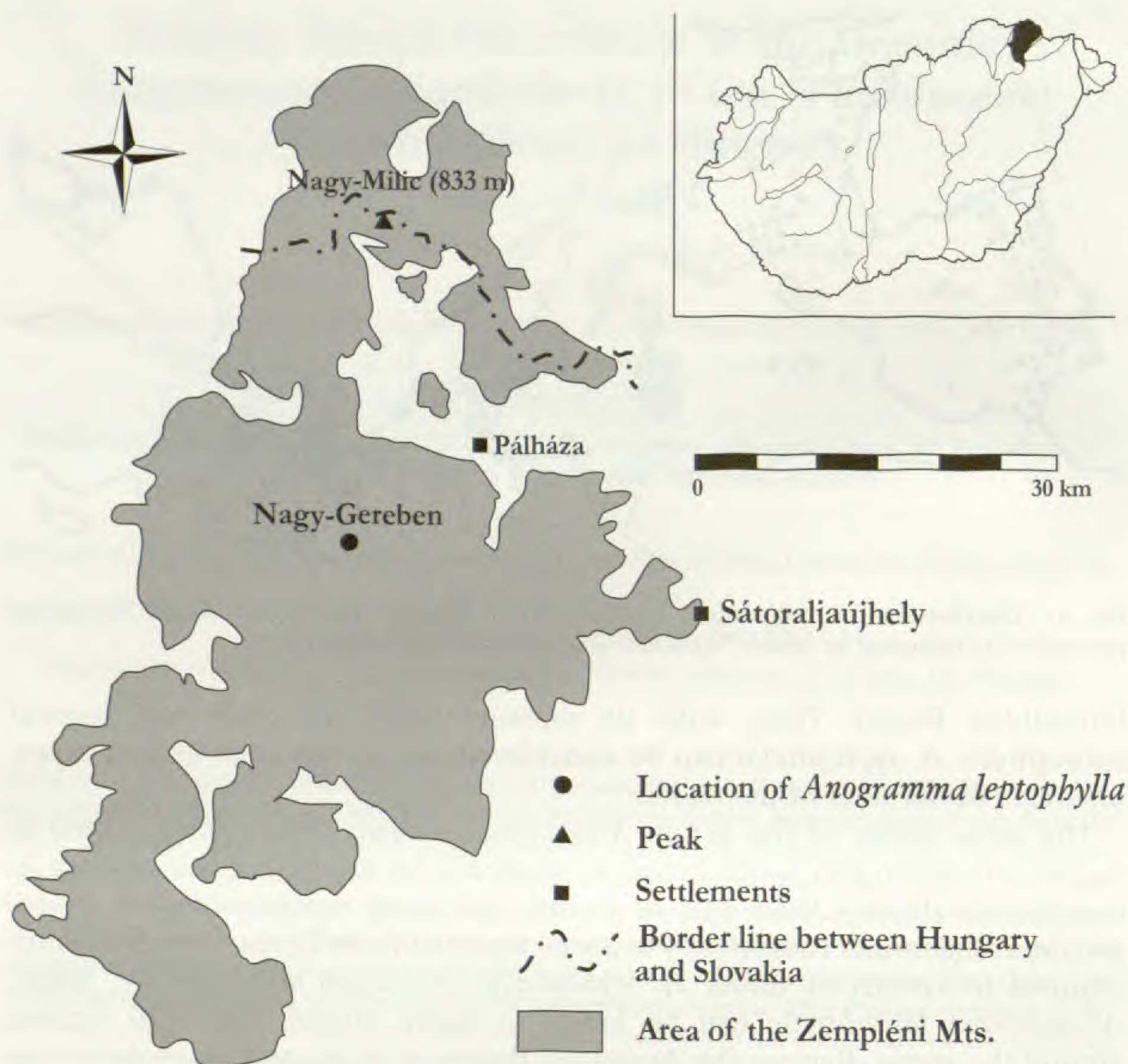


FIG. 2. Location of *Anogramma leptophylla* in Hungary.

In contrast to the above-mentioned, the Hungarian population at the village of Pálháza (Fig. 2) is unique in being situated in the inland region of the European continent ca. 1000 km from the nearest occurrences along the southern part of the Adriatic Sea and on the southern side of the Alps. It is one of the northernmost populations of this species in the world.

Although its presence in Hungary is unusual at first glance, the ecological requirements of this otherwise oceanic, subtropical, and tropical species are fulfilled by the microclimate of this location, which provides an air temperature above freezing and high humidity throughout the year. Some other European inland populations of *A. leptophylla*, such as those on the southern side of the Alps (in Switzerland and northern Italy), live at the mouths of caves (Chiodi, 1958; Hess *et al.*, 1976) that provide a suitable microclimate for the species. Our case is different, although some similarity may exist between the microclimate of caves and the talus crevices at Pálháza in that they may provide similar climatic conditions. During the winter of 2003



and 2004, our site was entirely covered by snow with the exception of the ca. 10 m<sup>2</sup> area where adult sporophytes of the fern grow, surrounded by green mats of mosses on the wet rocks.

This paper presents the characteristics (geological, microclimatological, and vegetational features) of the Hungarian population and the habitat preferences of *A. leptophylla* in the Carpathian Basin.

## METHODS

For insight into the microclimatic conditions of the habitat and to explore how *Anogramma leptophylla* can tolerate the unfavorable macroclimatic conditions, seasonal expedition field measurements (i.e., not repeated, but detailed observations of the climatic conditions that enable one to gain basic insight to the microclimatologic conditions of a site) were conducted at 12 designated points, which were intended to (i) reflect the characteristic features of the habitat itself and represent them in adequate density; (ii) permit comparison between the habitat and its environment, and (iii) represent points with various exposure, vegetation units, and soil coverage.

Measurements were carried out three times a day (at sunrise, around noon, and at sunset) on two different dates in 2005: at the height of sporophyte germination on February 19th, and at the height of spore ripening on April 3<sup>rd</sup>. The following parameters were determined: air temperature and relative humidity at a height of 2 m, soil temperature at depths of 2, 5, and 10 cm, and wind speed and direction at a height of 2 m. In addition to the above, air temperature and relative humidity were measured every 30 minutes, directly next to the sporophytes at the crevices of the substrate.

Air temperature and relative humidity were measured using a digital platinum resistance thermometer and capacitive hygrometer. Measurements of soil temperature were carried out using a digital platinum resistance thermometer suitable for measurements down to 10 cm, whereas wind speed was measured with a cup anemometer. Additionally, wind directions and microclimatological winds were determined.

The newly found population was visited regularly to observe its life-cycle. Because no species of similar life-strategy has been known in our region, the life-cycle of the fern was also examined. Growth studies, designed to investigate the impact of air humidity and water availability by watering and drying, were also carried out under laboratory conditions.

For chromosome counts, some adult sporophytes from the population were collected and transferred to a greenhouse. Chromosomes were counted from spore mother cells, following standard methods (Manton, 1950). Photographs were taken with a Leica microscope model DMRB.

## RESULTS AND DISCUSSION

*Lithology, climate and vegetation of the habitat.*—The population in the Zempléni Mountains (also known as the Eperjes-Tokaji Mountains) is located



along a roadside bank near the village Pálháza above the valley of Kemence Creek, on the hillside of Nagy-Gereben (Fig. 2) at 48°25'N, 21°25'E. The elevation is ca. 365 m above sea level. Exposure is to the east south-east (Fig. 5), and is the side of the hill most exposed to solar radiation. The population is found on talus slopes densely interlaced and developed on the rhyolite bedrock of the Pálháza-Telkibánya eruption center of the Lower Sarmatian volcanic cycle (Gyarmati, 1971). A road was cut in 1958 by forestry (Nagy Imre retired forester, *ex verb.*) into this unstable, rubble rhyolitic surface forming a moderately steep scree slope, which provides ca. 10 m × 1 m of habitat. The population fluctuates between ca. 400 and 800 sporophytes annually. The surrounding vegetation can be described as a habitat-complex of rocky grassland and debris slope forest all embedded in acidophilic hornbeam-oak woods with beech (Simon, 1977). A voucher specimen is deposited at the herbarium "Collectio Pteridophytorum" in the Hungarian Natural History Museum (BP) under the collection number "689786" (collecting date: 11.04.2001, collector: Csaba Molnár).

The annual precipitation of the sample area is ca. 700–750 mm (Mersich *et al.*, 2002), which is above the national average. Also, the highest values of relative humidity in the Hungarian context are found here in all seasons, approximately 75% during winter with values of actual evapotranspiration that may exceed 100 mm in July (Mersich *et al.*, 2002). Air temperature conditions of the Zempléni Mountains, with a mean annual temperature between 8.0 and 8.5°C at the northern regions, are among the coolest compared to other mountains of the North Hungarian Middle Range. As a whole, the climate of the region can be classified as cool and moderately humid (Justyák, 1998).

*Microclimatic conditions of the habitat.*—Results of microclimatological measurements indicate a positive anomaly both in air temperature ("heat outflow"; Fig. 5A) and relative humidity at the center of the locality, hereafter referred to as the "cauldron", i.e., the inner microclimatic space of the population location. The rise in temperature is quite conspicuous in winter seasons, when, unlike the surrounding area that is usually covered by significant snow cover, the cauldron is free of snow and manifestly unfrozen. Relative humidity remained constant at 100% between sunrise and sunset (Fig. 3). The permanently moist surface of the bedrock, and the water droplets on the surrounding moss-cushions also reflected saturated or over-saturated air present in the cauldron. At a distance of 2 m above the surface, a significant decrease in the diurnal course of relative humidity can be observed in front of the cauldron on the road (i.e., at the outer microclimatic space; Fig. 3). Here, the ca. 70% value after sunrise decreases until noon (to 44.6%), then it reaches ca. 65% at sunset. The values measured here compare well with the values of the remote measurement points (51.0–58.1% at noon, 55.5–61.3% at sunset). Thus, the outer microclimatic space reflects the characteristic values of the surrounding environment.

In the period following springtime thaw, a significant change was observed in the diurnal rhythm of relative humidity. The cauldron and its close



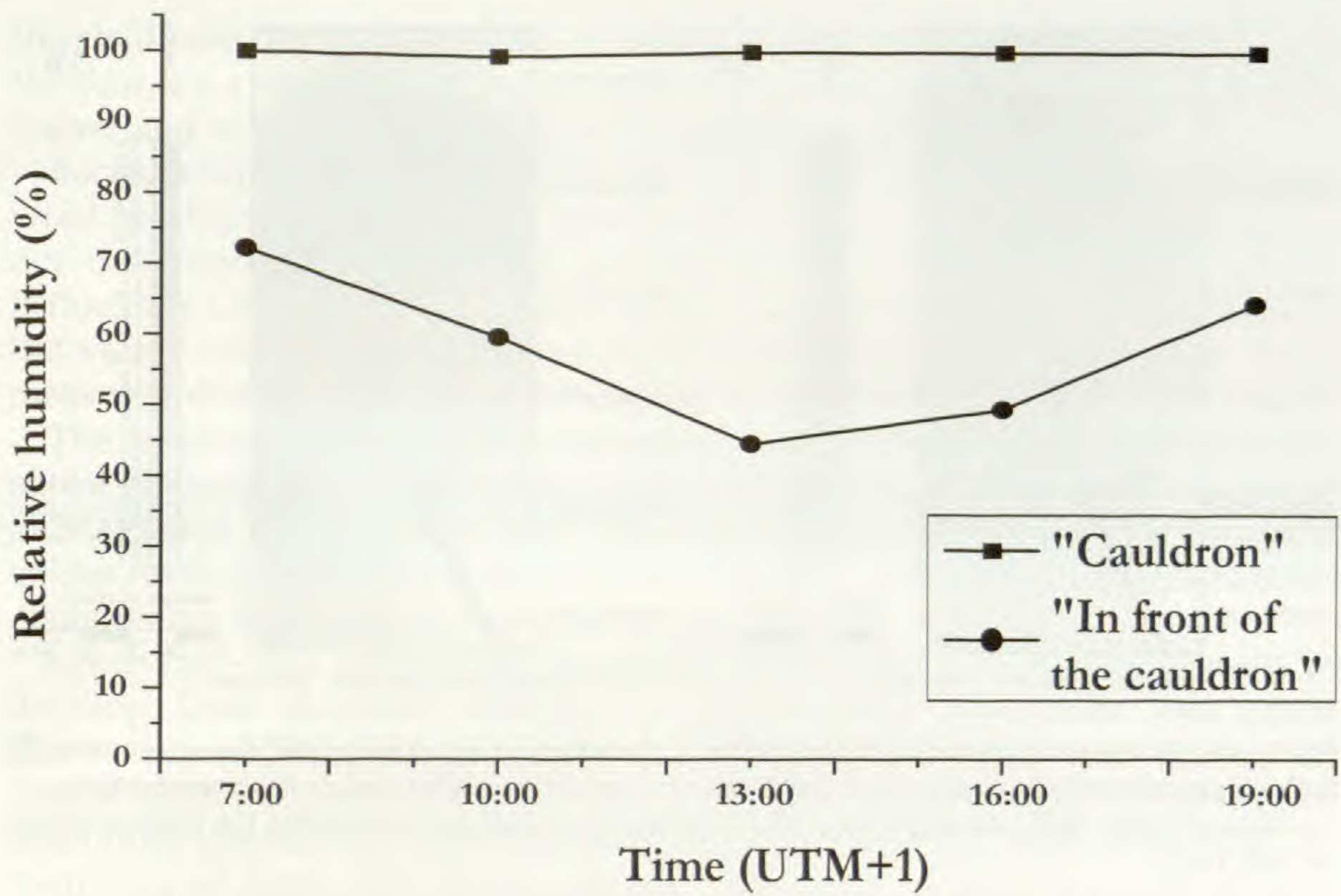


FIG. 3. The diurnal course of relative humidity at the sample area (19th February 2004).

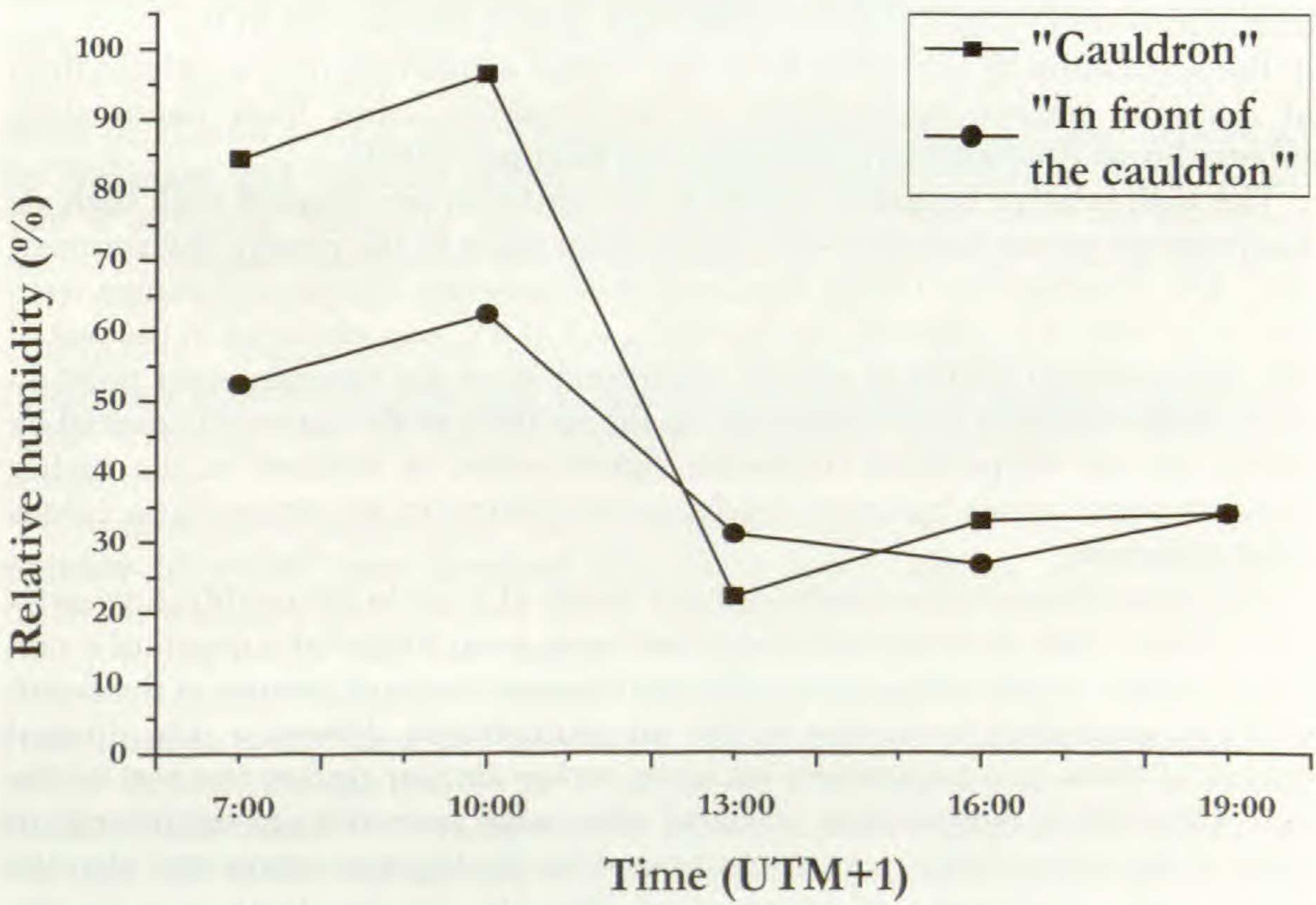


FIG. 4. The diurnal course of relative humidity after the spring thaw at the sample area (3rd April 2005).



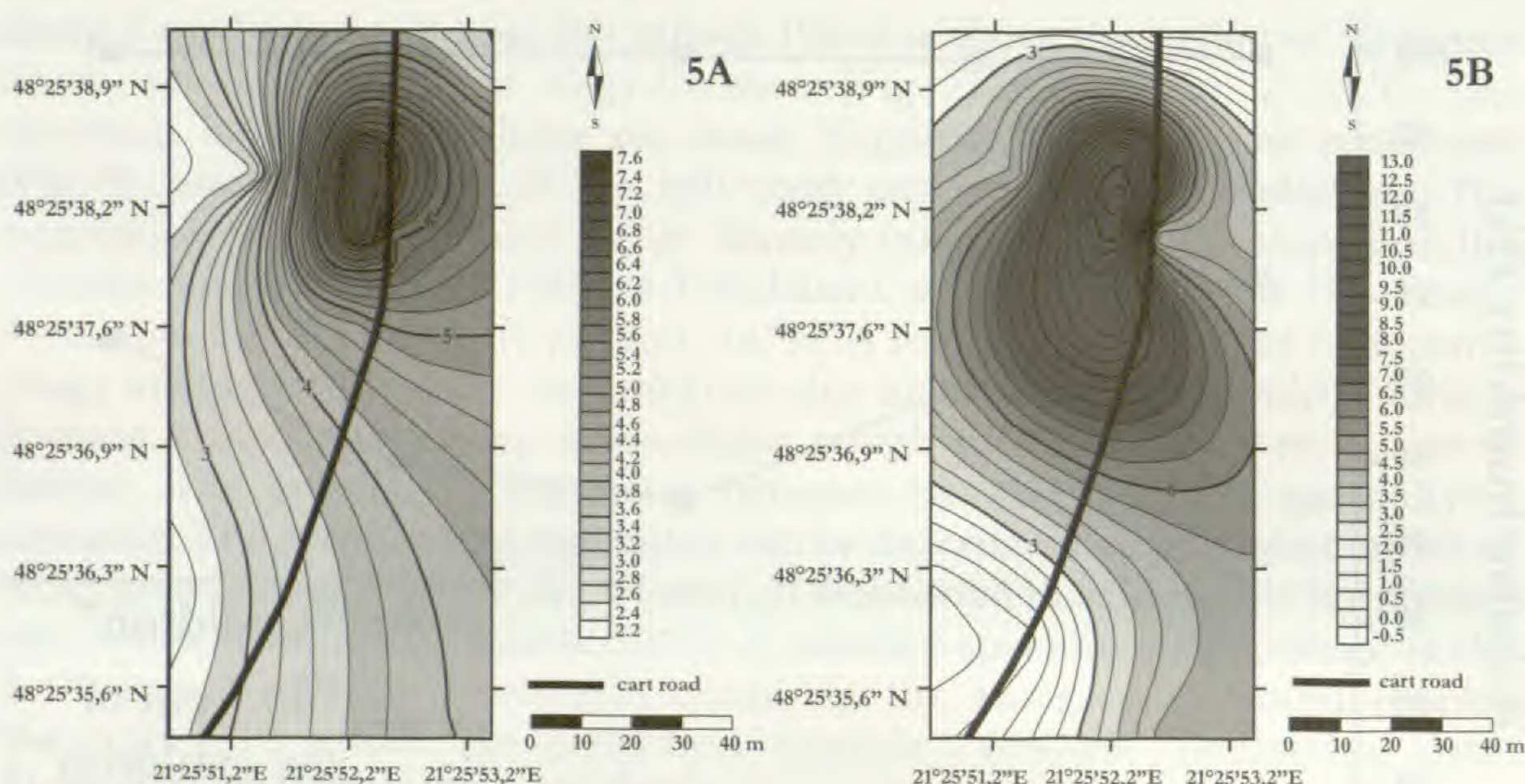


FIG. 5. A. Air temperature values of the habitat of *Anogramma leptophylla* and its environment. B. Soil temperature values measured in the depth of 5 cm at the habitat and its environment (both in °C; taken at noon, 19th February 2004). The habitat of the plant is delimited by the highest values on both maps.

environment switched to a different course that showed conspicuous congruency (Fig. 4). This phenomenon may be due to the cessation of the continuous water supply (snow-melt), that plays a crucial role in the existence of the population by providing mild and humid conditions during germination of dormant embryo sporophytes or gametophytic lobes from perennating tubercles as illustrated by Nakazato and Gastony (2003).

The high relative humidity values at the cauldron are coupled with high air temperature values that are 3–5 °C higher than those in the nearby environment (Fig. 5A). Temperature values measured here between sunrise and sunset were not lower than 4 °C, whereas, for example, 0.3–0.6 °C was observed at the rest of the measurement points at sunset. Additionally, at the measurement point in front of the cauldron (and close to it, on the sections of the cart-road covered by snow) the air temperature increased significantly, in contrast to the highly forested parts, where the most moderate oscillation in air temperature values were observed.

Soil temperature values measured at a depth of 2 cm in the cauldron were 7–11 °C higher than in its surroundings and were even higher at a depth of 5 cm. The increase in soil temperature after sunrise was the most intense at the depth of 2 cm, exceeding even that of the air temperature. However, the diurnal course of these two parameters becomes rather similar during the rest of the day. This rise in temperature occurred somewhat later at 5 cm depth and, in spite of this short delay, was characterized by the highest values and also the lowest daily fluctuation of temperature (Fig. 5B). At the depth of 5 cm the latter was between 9.1 and 11.9 °C, whereas the difference between the values measured at depths of 2 and 5 cm was only  $\pm 0.1$  °C, with greater variation at



the shallower depth. The results of measurements carried out in the vicinity of the fern, on a mat of moss at the most exposed side of the outcrop, indicated higher and also non-fluctuating soil temperature values.

Because air flow can counteract the high relative humidity, characteristic wind conditions of the sample area should also be mentioned. The results of our measurements showed the predominance of meso- and macroclimatic influences, i.e., a so-called channel effect in accordance with the orientation of the valley system. The mean values of wind speeds of 0.5 to nearly 1 m/s measured during the day indicate an intensive dehydrating effect.

The positive anomalies in temperature and relative humidity mentioned above diminished abruptly within even a few m distance from the *Anogramma* habitat patch. This was most probably due to the 0.5–1 m/s mean wind speed values resulting from the channel effect. This may cause the suitable habitat for *Anogramma* to be highly restricted to the cauldron.

*Life-cycle.*—The sporophyte generation of the studied population starts to develop from dormant embryos on perennating tubercles [see cover illustration of Nakazato and Gastony (2003)] in December, and during the crucial period of germination the above described specific microclimatological conditions provide favorable circumstances. Sporophytes reach maturity at the beginning of April, and spores are ripe from April to the beginning of June, then the sporophytes wither. Prothallia, newly produced from the spores, photosynthesize during June and July, and then, since no suitable growing conditions exist in this period, they form a perennating organ, a dormant tubercle, as found by Baroutsis (1976) and reported by Hagemann (1997) and Nakazato and Gastony (2003). The new sporophyte generation arises from these prothallia or from their dormant tubercles as explained and illustrated by Nakasato and Gastony (2003). Our greenhouse observations have shown that if adequate humidity and mild temperature (above zero) are provided under controlled conditions, the sporophytes can arise at any time in the year, and their life-cycle is completed within the same time as under natural conditions. Regarding our desiccation tolerance observations, dormant tubercles were found to be able to survive for 2.5 years in drought conditions. After watering, 5% of the prothallial tubercles immediately developed sporophytes.

*Chromosome counts.*—For the Hungarian population, the chromosome number of  $n=26^{\text{II}}$  was obtained (Fig. 6) in spore mother cells. However, different numbers are reported for *A. leptophylla* in the literature: Brownlie (1958) found  $n=29^{\text{II}}$  in New-Zealand, Tutin (Fabri, 1963) found  $n=26^{\text{II}}$  in the Channel Islands, Verma and Khullar (1965) found  $n=29^{\text{II}}$  in India, Mickel *et al.* (1966) found  $n=27^{\text{II}}$  and  $29^{\text{II}}$  in Mexico, Baroutsis and Gastony (1978) found  $n=29^{\text{II}}$  in South Africa and  $n=29^{\text{I}}$  in gametophytes from Mexico, Manton *et al.* (1986) found  $n=26^{\text{II}}$  in Madeira, and Queiros *et al.* (1988) found  $n=26^{\text{II}}$  in Portugal. Baroutsis and Gastony (1978) discussed the tendency of mitotic and meiotic chromosomes of *A. leptophylla* (including *A. guatemalensis* (Domin) C.Chr.) to stick together and observed thin and knob-like short chromosomes, factors potentially contributing to the variation in reported numbers. Some



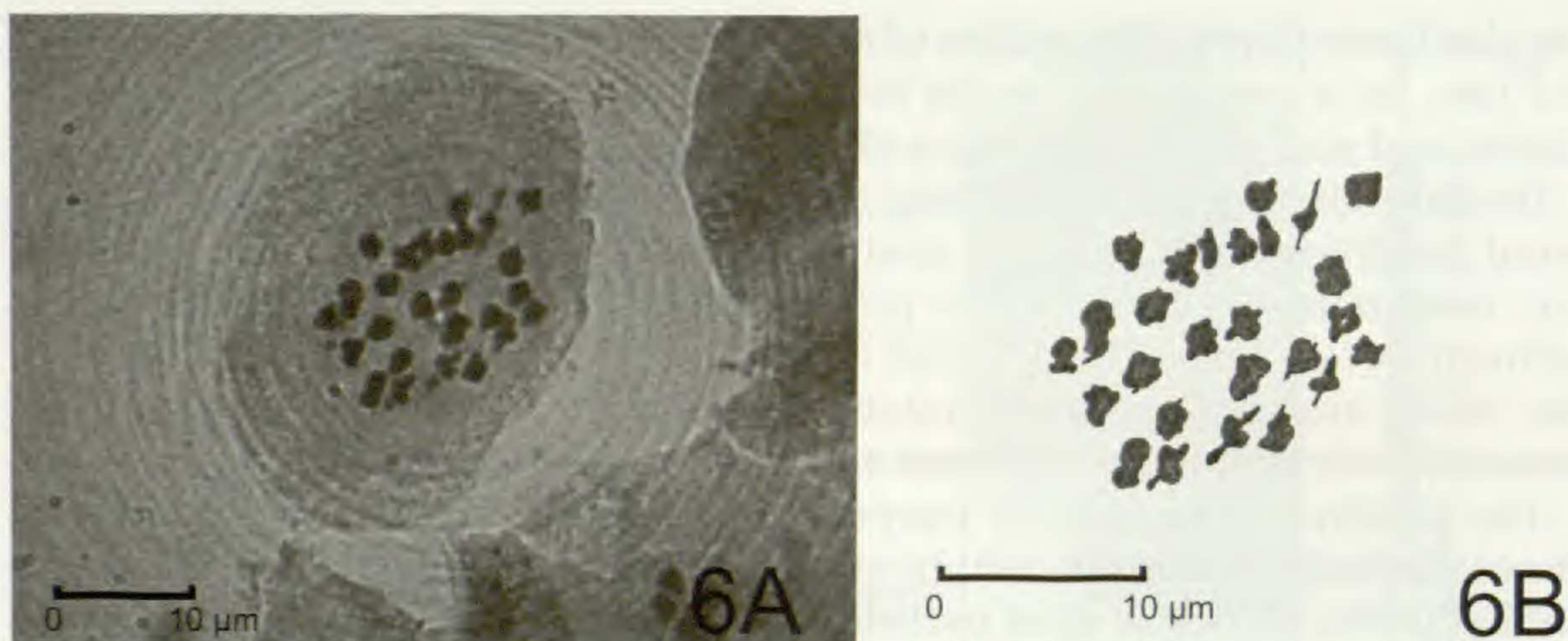


FIG. 6. Meiosis of spore mother cell in a studied *Anogramma leptophylla* ( $n=26^{\text{II}}$ ) individual. A. Original photograph. B. Schematic view of the previous.

larger chromosomes in the photograph of our specimen (Fig. 6.) can be observed. Rasbach and Reichstein (1990) and Lovis *et al.* (1993) re-examined the chromosome numbers in many populations, and they observed  $n=26^{\text{II}}$ . They concluded that many of the previously published counts are presumably incorrect, although, they urged further taxonomic research in two cases. Nakazato and Gastony (2003) noted that if the reinterpretation of chromosome number in *A. leptophylla* is correct, the number 26 is an apomorphic reduction in the common ancestor of their *A. leptophylla* clade from the plesiomorphic base number of  $n=29^{\text{II}}$  in Taenitidoid ferns. Thus, in spite of the cytological variability within the genus *Anogramma* (Gastony and Baroutsis, 1975), the world-wide distributed species *Anogramma leptophylla* seems to be uniform in this respect according to the re-examinations of Rasbach and Reichstein (1990) and Lovis *et al.* (1993). Our result is in line with these re-examinations, and the chromosome count of the Hungarian population supports the karyological homogeneity of the species.

**Conclusions.**—The surprisingly remote inland establishment of the extreme oceanic element *Anogramma leptophylla* in Hungary may be attributable to certain favorable environmental conditions. At the habitat of the species, special microclimatological conditions (higher air temperature and relative humidity values compared to its surroundings) can be observed at the very close surroundings of the population, hence providing suitable habitat for the colonization of the species. These conditions are strictly restricted to the close environment of the habitat, and their absence may not allow colonization elsewhere by *Anogramma* in the surrounding area. The life-cycle and the chromosome counts of the Hungarian population are in accordance with those reported for other European populations. The relatively recent colonization of the species is probable since the habitat was created by forestry in 1958 (Nagy Imre, *ex verb.*). The occurrence of *A. leptophylla* in this inland territory further contributes to our knowledge of the distribution of pteridophytes, where



similar isolated occurrences have been witnessed before. It also underlines the success and colonizing ability of this cosmopolitan species.

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